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A Statistical Model for Interpreting Neuroelectric Responses*

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Neuroelectric activity recorded after presentation of a controlled stimulus is called an "evoked response." Evoked responses are random, in that repeated presentations of a stimulus do not produce identical responses despite all effort to maintain identical conditions for all stimulus presentations. Responses may then be described statistically. The present model attempts to relate statistical characteristics of evoked responses, recorded by gross electrodes, to the statistical activity of the neural elements that contribute to the responses. The model postulates one or more populations of elements which, when they fire, contribute elemental waveforms to a gross response in which these waveforms are linearly summed. The statistical behavior of the elements in a population is described by their instantaneous firing rate, which is a function of time. In terms of the model, the statistical properties of the gross response (such as the mean and variance, both of which are functions of time) are shown to be related in a simple way to the instantaneous firing rates and elemental waveforms of the populations that contribute to the response. The model is an extension of the shot-noise model to time-variant phenomena; but some of the assumptions of the shot-noise model (specifically, statistical independence of firings) are relaxed.

I. INTRODUCTION

In neurophysiology recordings of various types of electrical potentials provide a monitor (albeit a very incomplete monitor) of the electrochemical events that characterize the operation of the system that is being studied. Progress in electrophysiology has been closely associated with developments in those engineering fields that provide its tools; recent advances in the design and production of oscilloscopes, amplifiers,

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pulse circuitry, and even of computers, have had a great impact on this science. But electrophysiologists who are interested in complex nervous systems are faced with a dilemma that overshadows the technical problems of improving electrodes, amplifiers, and recorders. Nervous systems (in man and other complex animals) contain many millions of neurons, interconnected and interacting in intricate fashion. These neurons have many different forms, and behave in different ways. This is the dilemma: When we are recording from microelectrodes that monitor the activity of one, or a few, of the neurons (no simple feat in itself) only a scant knowledge of the working of the system is gained, but when we are recording from gross electrodes that monitor responses of large numbers of neurons, individual events are difficult, or impossible, to decipher.

It would be very useful to have means for analyzing gross electrode potentials in terms of the activity of the neurons monitored by the electrode. A direct attempt to accomplish this has been made by simultaneous recording with gross electrodes and microelectrodes. This approach presents some difficulties, not the least of which is that the population of neurons sampled with microelectrodes may not be representative of the population that contributes potentials to the gross electrode.

The present work attempts to relate, by means of a mathematical model, statistical properties of the electrical potentials recorded by gross electrodes with the time-variant statistical activity of the populations of contributing neural elements. The properties of the elements are postulated in terms of a mathematical model that attempts to predict the way in which potentials of individual nerve cells or groups of nerve cells contribute to gross-electrode recordings.

There will be no attempt here to review experimental evidence that activity of nervous systems, especially of unanesthetized vertebrates, exhibits a great deal of randomness. We shall, however, mention briefly other mathematical models that are related to ours.

L. S. Frishkopf (1956) has postulated a model which, like the present one, is concerned with the statistical description of evoked responses (responses that are evoked by the presentation of discrete stimuli, usually sensory stimuli). He postulated populations of "neural units" with fluctuating thresholds. The units are defined abstractly and are only loosely related to physical structures. This model relates the distribution of thresholds of the units to the statistical properties of a summed "response." A mathematical model of ganglion cell discharge has been presented by R. Fitzhugh (1958). His model has statistical properties and is

also concerned with evoked responses. It treats the statistical response of a single cell in terms of decision theory.

In its formal mathematical structure the present model is a generalization of a model discussed by N. Campbell (1909), J. M. Whittaker (1937), and, most completely by S. O. Rice (1944, 1945). These authors were concerned with the statistical properties of noise that arises from shot effect in vacuum tubes or from thermal agitation of electrons in resistors. The shot-noise model treats the noise waveform as a summation of identical elemental pulse waveforms that result from electrons arriving at the anode of a vacuum tube. The statistical properties of the noise are related to the pulse waveform and the statistics of these arrivals. The model of Rice assumes a time-invariant probability of arrival of electrons, and independence between these events. In adapting the model to our purposes we have extended it to include time-variant processes, and the assumption of independence has been relaxed. C. E. T. Krakau (1956) has related the spectral characteristics of "neuronal time" series" to elemental waveforms in a model which, like ours, is closely related to that of S. O. Rice.

II. POSTULATES

In our model we deal with populations of "elements" with postulated mathematical properties. If we think of the "gross response" as a summation of small discrete potentials, the elements are postulated as the generators of these small elemental potentials.

Properties of Elements:

1. In any small unit of time Δt, an element may either "fire" or "not fire."

2. If an element fires in the interval $t' \leqq t < t' + \Delta t$, it contributes the elemental waveform $U(t - t')$ to the gross response $G(t)$.

A population of elements is an aggregate of elements with identical elemental waveforms.

Properties of a Population of Elements:

3. The probability that one of the elements of a population will fire during the interval $t' \leqq t < t' + \Delta t$ varies as the length of the interval for very short intervals. Thus,[1]

[1] Notation: $P_t(K, T)$ is the probability of K firings in a population during a time interval of length T sec, beginning at time t.

$$P_{t'}(1, \Delta t) = f(t') \, \Delta t. \tag{1}$$

4. It is assumed that in a very short interval, Δt, the probability that more than one unit in a population will fire, is negligible. Thus,

$$P_{t'}(0, \Delta t) + P_{t'}(1, \Delta t) = 1. \tag{2}$$

This postulate excludes synchronous firing of units, except as a limiting process.

It is shown in the Appendix that under conditions of independent firings (i.e., the probability of a number of firings in an interval is independent of the number of firings in any other interval) the model is an extension of the shot-noise model to the time-variant case, and that the firings follow a Poisson distribution. However, the assumption of independence is not usually applicable in considering populations of neural elements.

5. The gross response, $G(t)$, is the summation of contributed waveforms from the elements of one population or from a number of populations. The elemental waveforms are assumed to add linearly at the gross electrode and to be weighted equally.

III. RELATION OF SOME STATISTICAL PROPERTIES OF THE GROSS RESPONSE TO ELEMENT ACTIVITY (FOR ONE POPULATION)

A. The Instantaneous Firing Rate, $f(t)$

Given one population defined by our postulates, the way in which some statistical properties of the gross response $G(t)$ are related to the elemental waveform $U(t)$, and to the statistical parameter $f(t)$, are to be determined. First, $f(t)$ is shown to be the instantaneous firing rate of the population. The expected number of firings in the interval $0 \leqq t < T$ is

$$E_T[K] = \sum_{k=0}^{T/\Delta t} f(k\Delta t)\Delta t. \tag{3}$$

Let $k\Delta t = t$, and $\Delta t \to 0$, with t held fixed. Then

$$E_T[K] = \int_0^T f(t) \, dt. \tag{4}$$

Thus the average rate of firing,

$$\bar{n}(T) = \frac{E_T(K)}{T} = \frac{\int_0^T f(t)\,dt}{T}, \tag{5}$$

and $f(t)$ can be considered an instantaneous rate of firing.

B. Relation of the Mean of $G(t)$ to $f(t)$ and $U(t)$

The kind of electrophysiological experiment to which the present model applies is one in which a stimulus is presented and an evoked response is recorded. In order to obtain statistical properties of the evoked response, a number of responses are recorded under conditions that are as nearly identical as possible, and the statistical properties estimated. The simplest statistical property is the mean response. We shall show, now, in what way the mean response of the postulated model is related to $U(t)$, the elemental waveform, and $f(t)$, the instantaneous firing rate of the population, for the case of one population.

We consider, first, that the time scale is divided into very small intervals, Δt sec long, and define the random process

$$F(k\Delta t) = \begin{cases} \dfrac{1}{\Delta t} & \text{If an element of the population fires in the } k\text{th interval} \\ 0 & \text{If no element of the population fires in the } k\text{th interval.} \end{cases} \tag{6}$$

From postulates 2 and 5 the gross response, G, is seen to be a superposition of the elemental waveforms. Thus

$$G(n\Delta t) = \sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t)F(k\Delta t)\Delta t \tag{7}$$

where G and F are both discrete random processes. Taking the mean of both sides of Eq. (7), we obtain

$$\overline{G(n\Delta t)} = \sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t)\overline{F(k\Delta t)}\Delta t. \tag{8}$$

Then, from postulates 3 and 4, it follows that

$$\begin{aligned}\overline{F(k\Delta t)} &= f(k\Delta t)\Delta t \cdot \frac{1}{\Delta t} + [1 - f(k\Delta t)\Delta t] \cdot 0 \\ &= f(k\Delta t)\,.\end{aligned} \tag{9}$$

Substituting (9) in (8), we have

$$\overline{G(n\Delta t)} = \sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t) f(k\Delta t)\Delta t. \tag{10}$$

If we now let $n\Delta t = t$, $k\Delta t = \tau$, allow $\Delta t \to 0$, and hold t and τ fixed, we obtain the desired relation

$$\overline{G(t)} = \int_{-\infty}^{\infty} U(t - \tau) f(\tau)\, d\tau. \tag{11}$$

Hence, if we assume a single population, $\overline{G(t)}$ is the convolution of $U(t)$ and $f(t)$.

C. Relation of the Correlation Function of $G(t)$ to $f(t)$ and $U(t)$

Next consider the discrete random process

$$\begin{aligned}G(n\Delta t)G(m\Delta t) = \sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t)F(k\Delta t)\Delta t \\ \cdot \sum_{j=-\infty}^{\infty} U(m\Delta t - j\Delta t)F(j\Delta t)\Delta t.\end{aligned} \tag{12}$$

Taking the mean of both sides, we obtain

$$\begin{aligned}&\overline{G(n\Delta t)G(m\Delta t)} \\ &= R(n\Delta t, m\Delta t) = \sum_{k=-\infty}^{\infty} \sum_{j=-\infty}^{\infty} U(n\Delta t - k\Delta t)U(m\Delta t - j\Delta t) \\ &\qquad \cdot \overline{F(k\Delta t)F(j\Delta t)}\ \Delta t\Delta t.\end{aligned} \tag{13}$$

Consider $\overline{F(k\Delta t)F(j\Delta t)}$. For $k = j$.

$$\overline{F^2(k\Delta t)} = f(k\Delta t)\Delta t \cdot \left(\frac{1}{\Delta t}\right)^2 = \frac{f(k\Delta t)}{\Delta t}\,. \tag{14}$$

For $k \neq j$,

$$\overline{F(k\Delta t)F(j\Delta t)} = \left(\frac{1}{\Delta t}\right)^2 P\left(F(k\Delta t) = \frac{1}{\Delta t}, F(j\Delta t) = \frac{1}{\Delta t}\right). \tag{15}$$

If we assume $F(k\Delta t)$ and $F(j\Delta t)$ to be uncorrelated for all $k \neq j$, then

$$\overline{F(k\Delta t)F(j\Delta t)} = \overline{F(k\Delta t)} \cdot \overline{F(j\Delta t)} = f(k\Delta t)f(j\Delta t); \qquad k \neq j. \quad (16)$$

Hence, $F(k\Delta t)$ and $F(j\Delta t)$ are pairwise independent for $k \neq j$. It is well to note that this is a weaker condition than the requirement that the random process $F(k\Delta t)$ exhibit statistical independence for different values of the index k (Feller, 1957). Substituting (16) and (14) in (13), we obtain

$$\begin{aligned} R(n\Delta t, m\Delta t) &= \sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t)U(m\Delta t - k\Delta t)f(k\Delta t)\Delta t \\ &\quad + \sum_{\substack{k=-\infty \\ k\neq j}}^{\infty} \sum_{j=-\infty}^{\infty} U(m\Delta t - k\Delta t)U(m\Delta t - j\Delta t) \\ &\qquad \cdot f(k\Delta t)f(j\Delta t)\Delta t\Delta t \\ &= \sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t)U(m\Delta t - k\Delta t)f(k\Delta t)\Delta t \\ &\quad + \left[\sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t)f(k\Delta t)\Delta t \right. \\ &\qquad \left. \cdot \sum_{k=-\infty}^{\infty} U(m\Delta t - k\Delta t)f(k\Delta t)\Delta t\right] \\ &\quad - \sum_{k=-\infty}^{\infty} U(n\Delta t - k\Delta t)U(m\Delta t - k\Delta t)f^2(k\Delta t)(\Delta t).^2 \end{aligned} \quad (17)$$

Now let $n\Delta t = t_1$, $m\Delta t = t_2$, $k\Delta t = \tau$, and let $\Delta t \to 0$. Under the restriction that $f(t)$ remain finite, the last term on the right disappears, and we have

$$\begin{aligned} R(t_1, t_2) &= \int_{-\infty}^{\infty} U(t_1 - \tau)U(t_2 - \tau)f(\tau)\, d\tau \\ &\quad + \left[\int_{-\infty}^{\infty} U(t_1 - \tau)f(\tau)\, d\tau \cdot \int_{-\infty}^{\infty} U(t_2 - \tau)f(\tau)\, d\tau\right]. \end{aligned} \quad (18)$$

Using the result of Eq. (11), we can write Eq. (18) as

$$R(t_1, t_2) - \overline{G(t_1)} \cdot \overline{G(t_2)} = \int_{-\infty}^{\infty} U(t_1 - \tau)U(t_2 - \tau)f(\tau)\, d\tau. \quad (19)$$

If $t_1 = t_2 = t$, the following simple relation between the variance $\sigma^2(t)$, of $G(t)$, and $f(t)$ and $U(t)$ is obtained:

$$\sigma^2(t) = \overline{G^2(t)} - \overline{[G(t)]}^2 = \int_{-\infty}^{\infty} U^2(t - \tau) f(\tau)\, d\tau. \tag{20}$$

IV. RELATION OF SOME STATISTICAL PROPERTIES OF THE GROSS RESPONSE TO ELEMENT ACTIVITY (FOR MORE THAN ONE POPULATION)

There are numerous ways in which the properties of the present model differ from known neurophysiological mechanisms. Some of these differences are perhaps inevitable if the model is to retain mathematical simplicity. One of the most glaring differences between the abstractions of the model and the actualities of neurophysiology is the assumption of a single population of elements (employed to obtain the relationships in Section III). This assumption is easily extended to include the case of multiple populations.

To extend the model, $G(t)$ is assumed to be the summation of contributed waveforms from a number of populations with element waveforms $U_1(t)$, $U_2(t)$, $\cdots$ and instantaneous firing rates of $f_1(t)$, $f_2(t)$, $\cdots$. Now, we have random processes $F_1(k\Delta t)$, $F_2(k\Delta t)$, $\cdots$, where analogously with Eq. (6).

$$F_q(k\Delta t) = \begin{cases} \dfrac{1}{\Delta t} & \text{If an element of the } q\text{th population fires in the } k\text{th interval.} \\ 0 & \text{If no element of the } q\text{th population fires in the } k\text{th interval.} \end{cases} \tag{21}$$

Then the gross response

$$G(n\Delta t) = \sum_{k=-\infty}^{\infty} U_1(n\Delta t - k\Delta t) F_1(k\Delta t)\Delta t + \sum_{k=-\infty}^{\infty} U_2(n\Delta t - k\Delta t) F_2(k\Delta t)\Delta t + \cdots. \tag{22}$$

If we let

$$\begin{aligned} G_1(n\Delta t) &= \sum_{k=-\infty}^{\infty} U_1(n\Delta t - k\Delta t) F_1(k\Delta t)\Delta t \\ G_2(n\Delta t) &= \sum_{k=-\infty}^{\infty} U_2(n\Delta t - k\Delta t) F_2(k\Delta t)\Delta t \\ &\vdots \end{aligned} \tag{23}$$

we can write

$$G(n\Delta t) = G_1(n\Delta t) + G_2(n\Delta t) + \cdots . \tag{24}$$

By the averaging and limiting processes employed in Section 3, we obtain

$$\overline{G(t)} = \overline{G_1(t)} + \overline{G_2(t)} + \cdots . \tag{25}$$

If the random processes F_1, F_2, $\cdots$ are uncorrelated, the processes G_1, G_2 are uncorrelated, and it can be shown that

$$\begin{aligned} R(t_1, t_2) - \overline{G(t_1)} \cdot \overline{G(t_2)} = &\int_{-\infty}^{\infty} U_1(t_1 - \tau) U_1(t_2 - \tau) f_1(\tau)\, d\tau \\ &+ \int_{-\infty}^{\infty} U_2(t_1 - \tau) U_2(t_2 - \tau) f_2(\tau)\, d\tau + \cdots \end{aligned} \tag{26}$$

and that

$$\sigma^2(t) = \sigma_1^2(t) + \sigma_2^2(t) + \cdots . \tag{27}$$

where the statistical average without subscript is for the random process $G(t)$, and those with subscripts are for the processes $G_1(t)$, $G_2(t)$, $\cdots$.

V. DETERMINATION OF $U(t)$ AND USES OF THE MODEL

Thus far, we have dealt with three types of function: the statistics of responses recorded by a gross electrode; the firing rate, $f(t)$, of the population of elements contributing, in terms of our model, to the gross-electrode potential; and the elemental waveform $U(t)$. In analysis of electrophysiological data in terms of the model the statistics of the evoked responses would be estimated from experimentally recorded data.[2] The model then allows us to find the firing rates of the populations monitored by the gross electrode, if the pertinent elemental waveforms are known.

If the geometrical configuration of the neural elements contributing to the gross-electrode potential is sufficiently simple, it is possible to compute the elemental waveforms from theoretical considerations. An example would be recording from a bundle of parallel nerve fibers of one size, or of a number of sizes. For such conditions, the electrical properties of

[2] The estimation of statistical characteristics of response activity from experimentally recorded data and equipment for rapidly computing the estimates are discussed elsewhere (Communications Biophysics Group and W. M. Siebert, 1959).

the nerve impulse are sufficiently well known so that a good approximation of the elemental waveforms can be obtained. Usually, conditions are not so simple and an experimental approach must be used.

It is sometimes possible to stimulate the neural populations that contribute to the gross-electrode potential in such a manner that the elements of each population respond synchronously. It should be understood that synchronism is implied here in a relative sense; it is simply necessary that the time over which elements respond to the stimulus be very short compared with their $U(t)$. Electrical stimulation could provide a synchronous response, or, if responses are recorded from sensory systems, an impulsive stimulus such as an acoustic click, or flash, etc., might be appropriate. By repeating the stimulus, and averaging responses, one can obtain an estimate of the mean response, $\overline{G(t)}$, which for these conditions, will be proportional to the $U(t)$ of the (single) population, or the sum (with appropriate weighting factors) of the $U(t)$'s of the (multiple) populations contributing to the gross-electrode activity. This method does not indicate the number of populations contributing to the gross-electrode potential or give the decomposition of $\overline{G(t)}$ when a number of populations with overlapping $U(t)$'s are involved. Such information may be available from anatomical information, and from investigation of higher moments of the response.

When conditions are such that it is appropriate to consider higher-order statistics of responses in terms of the model, it is possible to use a self-checking feature to obtain a close fit of the model to experimental conditions. Thus, if the mean response to a stimulus is experimentally determined, and the elemental response, $U(t)$, is obtainable either from theoretical reasoning or from experimental evidence, an $f(t)$ can always be found under the assumption of a single population (i.e., by solving the integral equation $\overline{G(t)} = \int_{-\infty}^{\infty} f(\tau)U(t - \tau)\, d\tau$). The extent to which the single-population assumption is justified can be checked by employing the same experimental data for the determination of response variance. Comparison of this experimentally determined variance with the result of Eq. (20) indicates the fit of the single-population model, and if the assumption of one population does not fit the data, we can assume two populations (with $U(t)$'s consistent with our theoretical or empirical knowledge of the contributing neural elements) and by solving the appropriate integral equations find an $f_1(t)$ and $f_2(t)$ to fit the mean response and response variance. The assumption of two popula-

tions cannot be checked by computing the mean response and response variance alone, for there will always be some two-population model that fits these measures. However, the two-population model can be checked if the third central moment of the response is also computed. By the procedure of Sections III and IV one can show that for a single population,[3]

$$\overline{[G(t) - \overline{G(t)}]^3} = \int_{-\infty}^{\infty} U^3(t - \tau) f(\tau)\, d\tau \tag{28}$$

and that for multiple populations,

$$\overline{[G(t) - \overline{G(t)}]^3} = \int_{-\infty}^{\infty} U_1^3(t - \tau) f_1(\tau)\, d\tau + \int_{-\infty}^{\infty} U_2^3(t - \tau) f_2(\tau)\, d\tau + \cdots . \tag{29}$$

This "self-checking" feature should provide a close coupling between theoretical models and experimental data.

The model has been employed as an heuristic device in qualitatively interpreting results of experiments in which responses from the auditory nerve (near the round window), and auditory cortex of the nervous system of cats, were recorded by gross electrodes (Goldstein and Kiang, 1958; Goldstein, Kiang, and Brown, 1959). Questions of synchrony in the responses of neural elements and the ability of populations of neural elements to respond to repetitive stimuli were studied by analyzing the behavior of averages of evoked responses. For the conditions studied, a single population of neural elements was assumed. The waveform of the average of responses to clicks was used as $U(t)$. The equation relating mean gross response $\overline{G(t)}$ to $f(t)$ is the familiar superposition integral, and brings to mind an analogy with the equation relating input and response

[3] There is an extension of the assumption in (16), which is that for k, j, and m mutually unequal:

$$\overline{F(k\Delta t)F(j\Delta t)F(n\Delta t)} = \overline{F(k\Delta t)} \cdot \overline{F(j\Delta t)} \cdot \overline{F(m\Delta t)} = f(k\Delta t)f(j\Delta t)f(m\Delta t).$$

Also, the notion of pairwise independence must be similarly extended to independence by threes for the $F(k\Delta t)$ functions of the subpopulations. Expressions for higher moments may be obtained under appropriate assumptions of independence; however, the expressions for moments higher than the third become more complicated.

of a linear filter. In this sense, information contained in the mean gross response about instantaneous firing rate of a population is "filtered," and the impulse response of the filter is the elemental response of contributing elements. This analogy is useful for pointing out the limitations of studying temporal characteristics of neural activity by gross-electrode techniques.

A further use of the model is found in quantitative studies of the population structure and temporal response of units of the nervous system. The present mathematics lends itself to such quantitative study largely because it allows checking of any chosen model and provides means for a systematic extension of models as more data are obtained.

VI. CONCLUSION

In this paper we have referred to "elements" that contribute to a gross response. Since our primary interest has been in applying the model to specific neurophysiological experiments, there may be a temptation to equate the activity of these "elements" with that of nerve cells. This temptation should be avoided; although the postulated properties of the model relate to the way neural potentials contribute to gross-electrode recorded activity, there are apparent discrepancies even in trems of our present incomplete knowledge of the relevant neuroelectric phenomena.

One gross simplification is the assumption that the elemental potentials from a population (or populations) are weighted equally in the summation by the gross electrode. This overlooks the obvious factor of *orientation* of neural structures contributing to gross-electrode activity. The model could be extended to include a weighting factor to account for orientation and, in such a case, the relationship between the mean gross response and element activity would be essentially unchanged. $U(t)$ would represent an *average* (for the spatial orientation) element response. Although the relationships for the mean response would remain the same, the expressions for higher-order averages would lose their simplicity.

Another simplification is the postulate that when an element fires it always produces the same potential. This assumption is related to the all-or-nothing principle (Adrian, 1914) which may be restated: "A nerve fiber, stimulated, will fire to the maximum of its instantaneous ability if it fires at all" (Frishkopf, 1956). Perhaps a better title would be the "all-it's-got-or-nothing" principle. The deviations from a simple all-or-nothing principle are too complex to be examined here—suffice it to say that although some nerve potentials (principally, the action spike) are

usually close to all-or-none, others (the "graded" potentials) have essentially different characteristics (Eccles, 1957).

The present model is a continuation of the approach to a quantitative description of neuroelectric activity employed by McGill and Rosenblith (1951), Frishkopf (1956), and Frishkopf and Rosenblith (1958). It is of interest to examine the points of difference between our model and the others, especially the Frishkopf model. The Frishkopf model requires synchrony of evoked element firings and thus avoids detailed consideration of elemental wave shape. We have relaxed the requirement of synchrony (in fact in the present model synchronous firing of elements in a population may only be considered as a limiting process). In relaxing the requirement of synchrony we have been led to give consideration to the wave shape of the potentials contributed to the gross response by unit firings.

The Frishkopf model postulates statistical independence of neural units. As he points out, such an assumption may be a workable approximation for peripheral neurons but probably breaks down completely for the more central sections of the nervous system. [A probabilistic model for evoked responses from the cortex which does not assume statistical independence of neural elements has been developed by Macy (1954).] We have relaxed this postulate at the expense of obtaining a statistical description of population activity rather than element activity. In the present model, the degree of allowed statistical dependence of element activity depends on the statistical parameter that is under consideration. For example, in considering the mean response no degree of independence is postulated; in considering the response variance, pairwise independence of unit firings is postulated, and so on. It should be emphasized that pairwise independence is weaker than statistical independence. For pairwise independence, in a given time interval Δt that is very small, the probability of a unit firing is assumed to be independent of what happened in the population in any other *one* given very small time interval. Thus for large populations that are not "saturated" (with a number of unrefractive elements at all times), the assumption of pairwise independence is reasonable. The assumption of statistical independence postulates that the probability that an element will fire in a very small interval Δt would be independent of *all* other events.

However, if relaxing the requirement of statistical independence gives rise to the expectation that the model may "fit" closely the recordings by gross electrodes from the central nervous system, another obvious

simplification dampens it. The assumption that gross activity is composed of elemental potentials that are the same each time an element fires is especially tenuous for recording from the central nervous system, in which region "graded" potentials probably play an important role in determining the gross-electrode recorded potentials (Bullock, 1959). Indications that some of the graded potentials are all-or-nothing in their microstructure (Katz, 1950; del Castillo and Katz, 1956) are really not too comforting on this score.[4]

The present model should be considered as a small step in attempts to obtain a better understanding of neural activity recorded by gross electrodes. Perhaps sometime we shall have a "mathematical scalpel" which allows us to study simultaneously, and in detail, activity from many neural elements by recording from electrodes which do not have to be inserted deep into nerve tissue. But the present simple mathematical models of neural activity fall far short of this goal, and perhaps their greatest use is as indicators of the possibilities and limitations of methods of recording.

APPENDIX

The probability distribution of firings is derived in an analogous way to the probability distribution of electron-emission times in the shot-noise model in which $f(t)$ is a constant (Rice, 1944–45; Davenport and Root, 1958). Therefore we calculate, first, the probability of no firings in an interval of length T. Consider an interval beginning at $t = 0$, of duration $T + \Delta T$, to be broken up into two subintervals of durations T and ΔT. Under conditions of statistical independence,

$$P_0(0, T + \Delta T) = P_0(0, T)P_T(0, \Delta T). \tag{30}$$

Then, substituting from (1) and (2), we obtain

$$\frac{P_0(0, T + \Delta T) - P_0(0, T)}{\Delta T} + f(T)P_0(0, T) = 0. \tag{31}$$

As $\Delta T \to 0$, this difference equation becomes the differential equation

[4] For conditions in which the gross-electrode activity is largely a summation of graded activity, the elemental waveform $U(t)$ may be considered an *average* waveform for a given element without any complication of the expressions for the mean response resulting, but expressions for higher-order statistics become complex.

$$\frac{dP_0(0, T)}{dT} + f(T)P_0(0, T) = 0 \tag{32}$$

which has the solution

$$P_0(0, T) = \exp\left[-\int_0^T f(t)\, dt\right]. \tag{33}$$

Consider, next, the probability that K firings occur during an interval of length $T + \Delta T$, starting at $t = 0$. Again, we can break the interval into two adjacent subintervals, one of length T, and the other of length ΔT. If ΔT is short enough, there are only two possibilities during the subinterval of length ΔT; either one firing occurs during that interval or none occurs. Therefore, for small ΔT, assuming independence, we have

$$P_0(K, T + \Delta T) = P_0(K - 1, T)P_T(1, \Delta T) + P_0(K, T)P_T(0, \Delta T) \tag{34}$$

and substituting from (1) to (2), we have

$$\frac{P_0(K, T + \Delta T) - P_0(K, T)}{\Delta T} + f(T)P_0(K, T) = f(T)P_0(K - 1, T). \tag{35}$$

Then as $\Delta T \to 0$ we obtain the differential equation

$$\frac{dP_0(K, T)}{dT} + f(T)P_0(K, T) = f(T)P_0(K - 1, T). \tag{36}$$

The solution is

$$P_0(K, T) = \exp\left[-\int_0^T f(t)\, dt\right] \int_0^T f(t)P_0(K - 1, t) \cdot \exp\left[\int_0^t f(t')\, dt'\right] dt. \tag{37}$$

From this recursion equation we obtain the desired distribution

$$P_0(K, T) = \frac{\left[\int_0^T f(t)\, dt\right]^K \exp\left[-\int_0^T f(t)\right] dt}{K!} \tag{38}$$

When $P_T(1, \Delta T)$ depends on the number of firings in the interval $0 \geqq t > T$, the distribution will not have this simple Poisson form.

Under the assumption that firings are statistically independent Eqs. (11) and (20) are extensions of Campbell's Theorem (Campbell, 1909; Whittaker, 1937) to the time-variant case.

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